

## OBLIGATE AND FACULTATIVE SUSPENSION FEEDING IN ANURAN LARVAE: FEEDING REGULATION IN *XENOPUS* AND *RANA*

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### ABSTRACT

The obligate suspension-feeding *Xenopus laevis* larva can survive solely on particles over a wider concentration range, but the facultative suspension-feeding *Rana pipiens* complex larva has a greater behavioral plasticity in its feeding. Regulatory mechanisms for adjusting filtering and ingestion rates reflect the morphological differences between these tadpoles. *Xenopus* larvae regulated feeding primarily by altering buccal pumping rate and *Rana* by adjusting buccal volume. The feeding data for both species fitted a rectangular hyperbola, with a lower concentration "threshold," and were consistent with most predictions of "energy-optimization" models. The significance of a feeding "threshold" is discussed. Regulation by satiation may be a fundamental universal regulatory mechanism for feeding in phylogenetically-diverse suspension feeders. Negative allometry for buccal volume vs snout-vent length was noted for *Rana* and *Xenopus* larvae. Over all size classes, buccal volumes of *Rana* were smaller than those for *Xenopus*, confirming conclusions from earlier morphological studies. Over evolutionary time, the energetic consequences of different rates of supply of particles in temperate (*Rana*) vs tropical (*Xenopus*) waters, among other factors, may have selected for the observed differences in these tadpoles' feeding abilities. A number of behavioral adjustments, such as migration, metamorphosis, threshold feeding, and prey switching, may serve to minimize overexploitation of the prey of vertebrate suspension feeders, while insuring adequate food to supply energetic needs.

### INTRODUCTION

The most abundant and productive food source in aquatic ecosystems, microscopic suspended particles, generally can be exploited directly only by suspension feeders. A diversity of adaptations enable representative species from virtually all animal classes to entrap such particles (Jørgensen, 1966). However, analyses of this critical process have focused on zooplankton, numerically the most abundant suspension feeders. Comparative studies, in vertebrates as well as invertebrates, could lead to a more general understanding of the process of suspension feeding, its evolutionary significance, and its potential influence on planktonic organisms.

Anuran larvae are among the more versatile and efficient of the vertebrate suspension feeders, ingesting particles with diameters  $< 0.2 \mu\text{m}$  (Wassersug, 1972) to  $> 200 \mu\text{m}$  (Seale, 1980). The feeding dynamics of tadpoles are similar to those of zooplankton (Seale and Wassersug, 1979; Seale and Beckvar, 1980; Seale *et al.*, 1982). For any suspension feeder, at a given particle concentration,  $C$ , the filtering rate,  $F$ , is the volume of water cleared, and ingestion rate,  $I$ , is the corresponding

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Abbreviations:  $BV$ , buccal volume;  $C$ , particle concentration;  $CC$ , critical concentration;  $F$ , filtering rate;  $I$ , ingestion rate;  $P$ , pumping rate;  $SV$ , snout to vent length;  $TC$ , threshold concentration.

amount of food thus obtained, per unit time (see Mullin *et al.*, 1975). Mechanisms for adjusting  $F$  and  $I$  can be deduced from the tadpole's feeding process. Water is brought into the buccal cavity with a buccal pump; suspended particles are captured on gill filters and by a mucus-entrapment mechanism (DeJongh, 1968; Kenny, 1969; Gradwell, 1972a, b; Wassersug, 1972, 1980; Wassersug and Hoff, 1979). Hence, tadpoles can regulate  $F$  and  $I$  by adjusting: 1) pumping rate, 2) volume of water cleared per pump stroke (*i.e.* the buccal volume), and/or 3) entrapment efficiency (Seale and Wassersug, 1979; Wassersug and Hoff, 1979; Wassersug and Rosenberg, 1979; Seale *et al.*, 1982).

Anuran larvae offer a unique opportunity to compare mechanisms for feeding regulation in facultative *vs* obligate suspension feeders, within the same taxonomic order. With a few exceptions, the larvae of pipid frogs, such as the genus *Xenopus*, are obligate suspension feeders, whereas larvae of non-pipid frogs, such as the genus *Rana*, are facultative suspension feeders (Gradwell, 1971, 1972a, b, 1975; Wassersug and Hoff, 1979; Wassersug, 1980). In preliminary studies, obligate suspension-feeding *Xenopus* larvae regulated  $F$  and  $I$  primarily by varying buccal pumping rate and *Rana* larvae mostly by adjusting buccal volume and to a lesser extent by adjusting pumping rate (Seale and Wassersug, 1979; Wassersug and Hoff, 1979; Seale *et al.*, 1982). Morphological differences in these larvae were consistent with experimental results (Seale and Wassersug, 1979; Wassersug and Hoff, 1979; Seale *et al.*, 1982), providing a partial confirmation of these differences in feeding regulation. However, the experiments could be criticized in some respects. First, the comparisons were not made under identical conditions: 1) *Rana* larvae were field collected but *Xenopus* larvae were laboratory raised; 2) *Rana* larvae were conditioned longer than *Xenopus* larvae; and 3) the containers allowed for settling differences, *e.g.* between experimental and control vessels. Secondly, earlier studies used *R. sylvatica*, an atypical *Rana* larva. Most *Rana* larvae are characteristically benthic, whereas *R. sylvatica* larvae have morphological traits more commonly seen in midwater larvae which are primarily adapted for entrapping planktonic organisms (Wassersug and Hoff, 1979).

Here I describe experiments incorporating improvements in methodology to examine regulation of feeding in the larvae of *Xenopus laevis*, the South African clawed frog, and of two species in the *Rana pipiens* complex, leopard frogs, representing "typical" *Rana* tadpoles (Wassersug and Hoff, 1979). In most respects, the data confirmed previous findings (see above). Results are discussed in relation to predictions and assumptions of general models of suspension feeding, and to the potential effects and evolutionary significance of vertebrate suspension feeders in aquatic ecosystems.

## MATERIALS AND METHODS

### *Suspension-feeding dynamics*

Anuran larvae were raised from fertilized eggs in the laboratory. *Rana pipiens* adults were purchased by J. Turpen from the Lemberger Co., in Wisconsin. The species identification was verified from adult characters (Pace, 1974). *Xenopus laevis* larvae were obtained from E. Hibbard. The *X. laevis* larvae were fed solely on yeast, *Saccharomyces cerevisiae*, the experimental food. The *Rana* larvae were raised on commercial fish food, but were fed exclusively on yeast suspensions for at least 3 weeks prior to experiments. All tadpoles were in Gosner (1960) stage 40 or earlier.

As an improvement over previous experimental design (Seale and Wassersug,

1979; Seale and Beckvar, 1980; Seale, *et al.*, 1982), the grazing chambers incorporated a circulating sidearm (modified from Ričica, 1966), which minimized differential settling between experimental and control chambers, and between the two species of larvae. The chambers were constructed from 250 ml plastic, screw-capped, inverted Erlenmeyer flasks, with their normal bottoms removed. A screen was placed diagonally about 0.5 cm above the edge of the screw cap in each flask; this barrier prevented the tadpole from swimming into the flask's neck, and isolated settled fecal matter from the animal. A "Y"-tube sidearm was attached to two 3 mm I.D. plastic tubes inserted into each flask; one was about 1 cm above the screen, and the other was vertical above the first and about 1 cm below the open top. The base of the "Y" tube was attached through vinyl tubing to an aeration pump. Activation of the pump caused water to circulate from the bottom of the chamber through the sidearm, and then to exit with a gentle pulsatile action through the top tube. These modifications allowed circulation and aeration of the yeast without producing strong currents or bubbles within the chambers.

Tadpoles were acclimated to experimental conditions and prefed on yeast for at least 24 h prior to each experiment. Within 2 h of each experiment, fresh yeast suspensions were made from dried, commercial yeast in dechlorinated tap water. Three experimental (one tadpole each) and one control (no tadpole) chambers were monitored simultaneously. Experiments were conducted in the light at  $20.0 \pm 0.5^\circ\text{C}$  for 4–10 h, beginning in early afternoon. Data collection was delayed for 1 h because after handling, respiration (Feder, 1981) and feeding (Wassersug and Hoff, 1979; Seale and Beckvar, 1980) rates were erratic for at least 45 min in earlier studies. Mean pumping rate (number of buccal depression  $\cdot \text{min}^{-1}$ ) was obtained from at least 6 independent visual estimates on each animal at sampling time, using a stopwatch. After measuring pumping rates, but before taking yeast samples, I scraped the interior of each chamber with a rubber rod, using extreme caution not to disturb the animal. Samples from the chambers were processed for counting, and biovolumes were standardized, as previously described (Seale and Wassersug, 1979; Seale and Beckvar, 1980).

An electronic particle-counting system was used to enumerate and concurrently to obtain a total biovolume (wet cell volume) for each yeast sample (see below). The system incorporated several improvements over the one used in earlier studies (see Seale and Wassersug, 1979; Boraas, 1980; Seale and Beckvar, 1980). It consisted of a Model ZB Coulter Counter with external manometer stand, interfaced with a C-100 Channelyzer through a modified Coulter teleprinter interface to a microcomputer. The modifications needed to route signals from a Channelyzer through a Teleprinter interface to a microcomputer, rather than a teletype, are relatively simple; the design and software for our system is available upon request (see acknowledgments). This system allowed for rapid data collection and storage for later manipulations, as well as immediate on-line computation of total number and biovolume. Transmission errors were detected by comparing the Channelyzer reading to the computer readout for number. The Coulter Counter was subject to inaccuracies at  $C$  below  $5\text{--}9 \times 10^4 \mu\text{m}^3 \cdot \text{ml}^{-1}$  because of background. Electronic noise contributed to this background, which varied from day to day; this is a source of error in all electronic particle-counting systems.

The tadpole filtering rate,  $F$ , was computed indirectly from yeast concentration, and ingestion rate was computed as  $FC$ , as previously described (Seale and Wassersug, 1979; Seale and Beckvar, 1980). The mean yeast concentration,  $C$ , was estimated as  $(C_1 - C_0) / \ln(C_1/C_0)$ , where  $C_0$  is the yeast concentration at the beginning and  $C_1$  that at the end of the sample interval. This indirect method for

estimating filtering rate assumes an exponential decline for  $C$  during each sampling interval, and 100% efficiency of particle retention, which may not be valid under all conditions (see Coughlan, 1969; Seale and Wassersug, 1979; Seale and Beckvar, 1980; Seale *et al.*, 1982). Tadpole buccal volumes were estimated by dividing filtering rate by pumping rate for each time interval. Since the tadpoles' responses to  $C$  might be affected by the amount of time they had spent in the chambers, the initial  $C_0$  was varied for each experiment. After at least 2 sampling intervals,  $C$  was raised by adding a portion of a 1% yeast suspension and the chamber sampled for at least one more time interval. Based on previous results (Seale and Wassersug, 1979),  $C$  was expressed as biovolume  $\cdot \text{ml}^{-1}$  and  $I$  was computed in terms of  $(\mu\text{m}^3 \text{ of yeast}) \cdot (\text{tadpole g wet mass})^{-1} \cdot \text{h}^{-1}$ .

Parameter estimates for nonlinear equations were obtained by nonlinear regressions on the data as previously described (Seale and Beckvar, 1980; Seale *et al.*, 1982). Parameter estimates were selected after an examination of standardized residual plots (Neter and Wasserman, 1974).

In this paper, all errors are presented as  $\pm 95\%$  confidence intervals.

### *Buccal volume as a function of individual size*

Upon the completion of the feeding studies described above, I examined the relationship between individual size and apparent buccal volume for larvae of *X. laevis* and of *R. pipiens* complex in more detail. These studies were initiated in late spring, when *R. pipiens* adults no longer were available for laboratory fertilization. I obtained a fresh clutch of *R. sphenoccephala* (= *R. utricularia*; see Pace, 1974), the southern leopard frog, from the Pine Barrens near Hammonton, New Jersey. This is the only leopard frog in this region (Conant, 1975).

Both the *Rana* and the *Xenopus* larvae were raised on yeast from hatching. Individuals from each of these two growing cohorts were selected at random on dates of experiments. All tadpoles were in Gosner (1960) stages 26–40. Experiments were conducted as described above, except that the animals were allowed to acclimate for at least 2 h before sampling, and only two intervals were sampled for each tadpole. The narrow concentration range examined ( $3\text{--}6 \times 10^7 \mu\text{m}^3 \cdot \text{ml}^{-1}$ ) corresponded to particle densities where both larval species maintained relatively constant buccal volumes in previous experiments, displaying "normal" contractions of the buccopharyngeal musculature (Seale and Wassersug, 1979). Wet mass of most live animals was measured (after being gently blotted with a paper towel) to the nearest 0.01 g with a triple-beam balance, following the completion of each experiment. The smallest tadpole size class was weighed to the nearest mg with an analytical balance, in tared containers containing water (0.5–2.0 ml).

### *Experimental advantages of anuran larvae for studying the process of suspension feeding*

The behavioral responses of tadpoles to particulate food (e.g. pumping rate adjustments) often can be observed directly (also see Seale and Wassersug, 1979). Filtering and ingestion rates can be estimated on single tadpoles, eliminating crowding effects and allowing individual variability to be assessed. Tadpole feeding responses are similar across food types, minimizing confounding effects of selective feeding (Seale and Beckvar, 1980). Individual tadpoles can cause detectable reductions in particle concentrations inside grazing chambers within a matter of minutes rather than of hours. Hence, the duration of tadpole feeding experiments can be less than one division time of the prey organism. This minimizes the con-

founding effect of prey growth in control and experimental chambers, a serious problem in zooplankton studies (Donaghay and Small, 1979). Data from the tadpoles (e.g. Seale and Beckvar, 1980; Seale *et al.*, 1982) provide a relatively clear-cut assessment of the shapes of feeding curves, compared to zooplankton data sets (e.g. Frost, 1975; Mullin *et al.*, 1975; Donaghay and Small, 1979), in part because the concentration ranges for tadpole feeding encompass several orders of magnitude, including those where electronic particle counters give reliable data above background.

## RESULTS

### *Suspension-feeding dynamics*

The larvae of *Rana pipiens* and *Xenopus laevis* displayed similar patterns of change in filtering rate,  $F$ , and ingestion rate,  $I$ , as functions of continuously varying concentration  $C$  (Fig. 1). However, there were several species-specific differences, particularly in the behavioral mechanisms used to regulate feeding (Fig. 2). The primary response to changes in  $C$  of the *Xenopus* larva was an adjustment in pumping rate,  $P$ , and that of *Rana* was an adjustment in buccal volume,  $BV$  (Fig. 2). These general relationships are described more fully below. There was no significant difference ( $t$  test;  $P > 0.05$ ) in the average wet mass of larvae of the two species, *R. pipiens* ( $1.19 \pm 0.49$  g;  $n = 7$ ), and *X. laevis* ( $1.29 \pm 0.26$  g;  $n = 15$ ). Since variables ranged over several orders of magnitude, in this paper data are plotted as log transformations for maximum resolution in lower ranges.

Using the convenient terminology of Mullin *et al.* (1975), the  $F$  peaked at an intermediate "critical" concentration ( $CC$ ) and declined at both higher and lower concentrations (Fig. 1A), in both species. Below the "threshold" concentration ( $TC$ ), the estimates for filtering rates were zero. The  $I (=FC)$  was a direct, nonlinear function of  $C$  (Fig. 1B), increasing from zero at the  $TC$  and asymptotically approaching a maximum ( $I_{max}$ ) at very high  $C$ . These patterns in  $I$  and  $F$  are consistent with several models previously used to describe zooplankton feeding (Mullin *et al.*, 1975; and further discussion below).

In the presence of tadpole grazing, the  $C$  eventually stabilized at a low concentration. Since the indirect method results in a positive estimate of  $F$  only with detectable changes in  $C$  through time, this stabilization resulted in an estimate of zero for  $F$  at low  $C$  (Fig. 1). Observations of zero  $F$  are plotted as  $0.01 \text{ ml} \cdot \text{g}^{-1} \cdot \text{h}^{-1}$  on the log-log plot in Figure 1. The concentrations where estimates of  $F$  approach zero designate "thresholds" for individual tadpoles (Fig. 1A). A tadpole placed in a yeast suspension at or below its  $TC$  caused no further reductions in yeast concentrations, but continued regular buccal pumping (Fig. 2). Hence, some yeast-laden water necessarily was being passed over the tadpole's buccopharyngeal particle-entrapping surfaces. These observations suggest that the efficiency of particle retention was reduced at low  $C$ , and that the filtering rates and buccal volumes (estimated as  $F/P$ ) shown here are minimum estimates (also see Seale, 1981).

For each species, the filtering rate peaked in the vicinity of a "critical"  $C$ , the  $CC$ . The  $CC$  for *Rana* was an order of magnitude higher than that for *Xenopus* larvae (Fig. 1A). There was a great deal of variability in the  $C$  where individual tadpoles displayed their peak  $F$ . By analyzing residual plots of piecewise regressions (after Neter and Wasserman, 1974) on log-transformed data, the  $CC$  of each species was estimated (Table I). The estimated slopes of the lines describing the relationship between  $F$  and  $C$  were not significantly different for the two larval

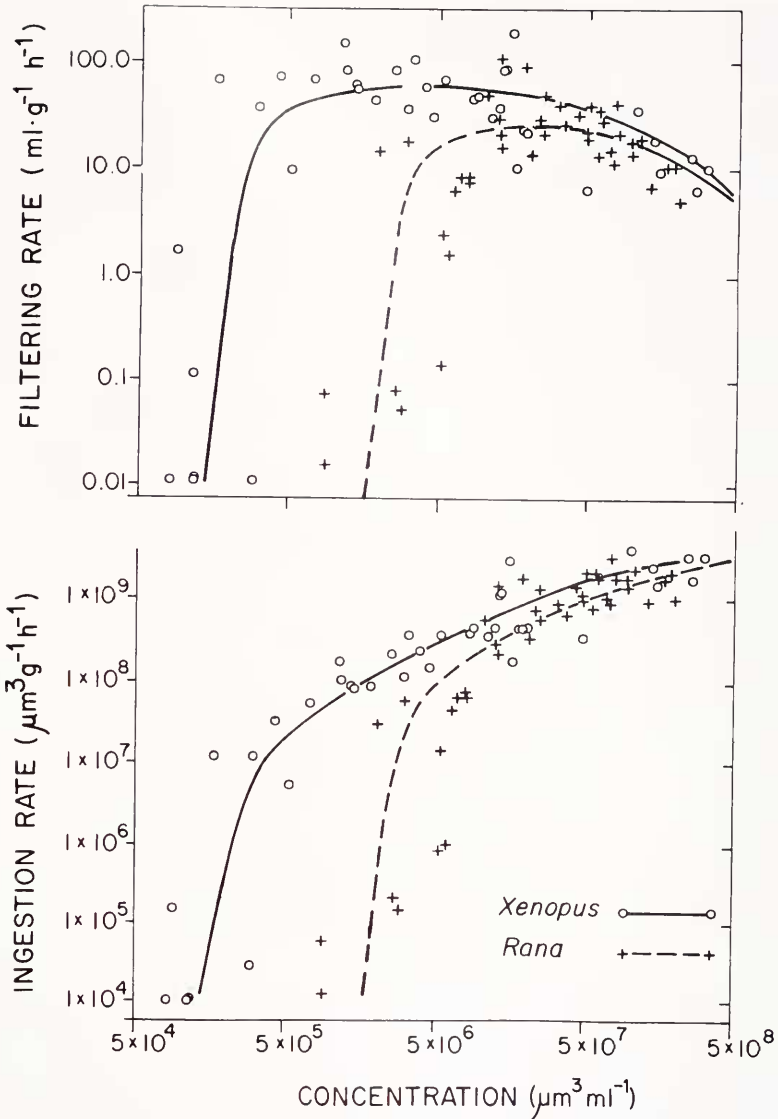


FIGURE 1. Feeding responses of *Xenopus laevis* and *Rana pipiens* larvae, as functions of continuously varying yeast concentrations. Morphologically, these two species represent extremes in feeding adaptations. Reductions in concentration through time were caused by tadpole feeding. An electronic particle counter was used to obtain indirect estimates of filtering (top) and ingestion (bottom) rates. Estimates assumed an exponential decline in yeast concentration through time and 100% particle retention. The fitted lines show the patterns of filtering and ingestion rates predicted by the Monod (Michaelis-Menten) model with a threshold:  $I = I_{\max} (C - TC) / [K_{1/2} + (C - TC)]$ , where  $I$  is the ingestion rate,  $I_{\max}$  is the maximum ingestion rate,  $K_{1/2}$  is the "half-saturation constant",  $C$  is the mean yeast concentration over each sampling interval, and  $TC$  is the "threshold" concentration. Model predictions for  $F$  were derived as  $I/C$ . According to the model, ingestion rate is half-maximum at  $K_{1/2} + TC$ . Parameter estimates used for plots were for *Rana*:  $I_{\max} = 2.9 \times 10^9 \mu\text{m}^3 \cdot (\text{g wet mass})^{-1} \cdot \text{h}^{-1}$ ,  $K_{1/2} = 8.8 \times 10^7 \mu\text{m}^3$ , and  $TC = 1.9 \times 10^6 \mu\text{m}^3$ ; and for *X. laevis*:  $I_{\max} = 3.0 \times 10^9 \mu\text{m}^3 \cdot (\text{g wet mass})^{-1} \cdot \text{h}^{-1}$ ,  $K_{1/2} = 4.3 \times 10^7 \mu\text{m}^3$ , and  $TC = 1.9 \times 10^5 \mu\text{m}^3$ . Of course, individual variability and experimental conditions can alter these "parameters", and other mathematical expressions for these responses can be formulated.

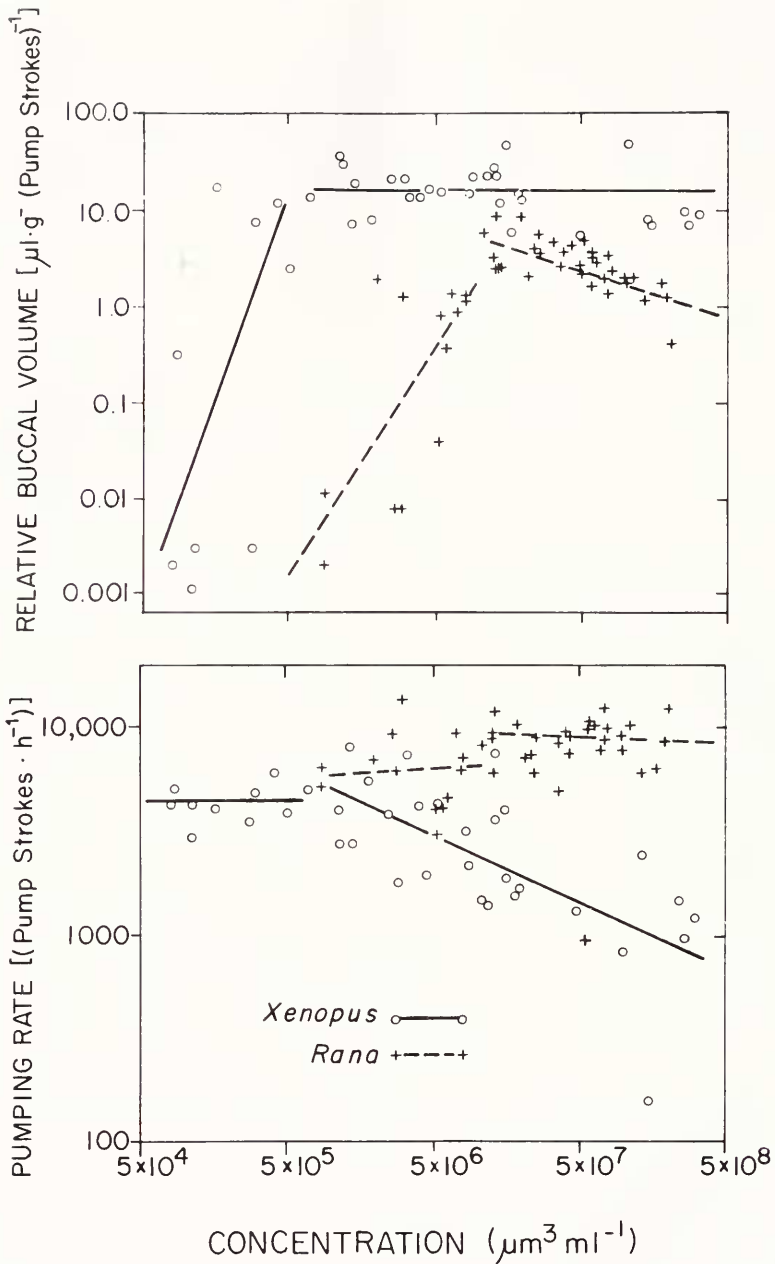


FIGURE 2. Differences in behavioral mechanisms used to regulate feeding by facultative (*Rana*) and obligate (*Xenopus*) suspension-feeding tadpoles. The major response of *X. laevis* larvae to changes in  $C$  was an adjustment in buccal pumping rates. *R. pipiens* larvae responded to changes in concentration primarily by altering their apparent buccal volume (volume cleared/pump stroke), apparently by adjusting contractions of buccopharyngeal muscles as well as particle entrapment efficiency. Fitted lines show piecewise linear regressions to the log-transformed data, using the "critical" concentration (Table I) as the point of discontinuity (parameter estimates in Table I).

species, either above the  $CC$  ( $P > 0.05$ ), where the slopes for  $\log F$  vs  $\log C$  were negative for both, or below the  $CC$  ( $P > 0.05$ ), where they were positive for both species (data in Table I).

The two species made these similar adjustments in  $F$  through different behavioral mechanisms: *Xenopus* larvae primarily regulated pumping rates, and *Rana* larvae buccal volumes (Table I; Fig. 2). With increasing  $C$ , the pumping rate,  $P$ , of the *Xenopus* larva declined exponentially from maximum at the  $CC$ , causing a significant negative relationship between  $\log P$  and  $\log C$  but not in *Rana* (Table I). Below the  $CC$ , neither species altered pumping rate significantly with changing  $C$  (Table I). For the *Rana* larva, buccal volume was a negative function of  $C$  above the  $CC$  but not for the *Xenopus* larva (Table I). Below the  $CC$ ,  $BV$  was a positive exponential function of  $C$  in both species (Table I). Filtering rates declined much more rapidly than pumping rates as tadpoles reduced  $C$  below their  $CC$  (Figs. 1, 2), causing this positive  $BV$  vs  $C$  relationship. The rapid reductions in  $BV$  probably resulted from reduced particle entrapment efficiency. Filtering rates may be altered by adjusting the contractions of buccopharyngeal muscles and by changing entrapment efficiencies (Seale and Wassersug, 1979; Seale *et al.*, 1982).

In both species,  $I$  asymptotically approached a maximum above the  $TC$  (Fig. 1B). The mean of the highest observed ingestion rates, as  $\mu\text{m}^3 \cdot (\text{g wet mass})^{-1} \cdot \text{h}^{-1}$ , of the *R. pipiens* larvae fed on yeast ( $1.59 \pm 0.30 \times 10^9$ ;  $n = 19$ ) was not significantly different ( $t$  test;  $P > 0.05$ ) than those of *R. catesbeiana* fed on algae ( $1.15 \pm 0.41 \times 10^9$ ;  $n = 6$ ) in a previous study (Seale and Beckvar, 1980). Also, the mean highest ingestion rate for yeast by the *X. laevis* larvae ( $2.88 \pm 0.77 \times 10^9$ ;  $n = 7$ ) in this study was not significantly different ( $t$  test;  $P > 0.05$ ) than for algae ( $3.43 \pm 1.55 \times 10^9$ ;  $n = 5$ ) in the earlier study (Seale and Beckvar, 1980). In this study, using tadpoles well acclimated on yeast, the mean of highest ingestion rates for *Rana* and *Xenopus* larvae were not significantly different from each other ( $t$  test;  $P > 0.05$ ). These maximum ingestion rates were intermediate between previous estimates for *Rana* and *Xenopus* fed on algae, where significant differences were noted (Seale and Beckvar, 1980). This suggests that the different acclimation procedures used for tadpoles of these two genera could have resulted in the species differences in maximum feeding rates observed previously (Seale and Beckvar, 1980).

Our data on the ingestion rates of *Rana* and *Xenopus* larvae vs concentration were fitted (after Mullin *et al.*, 1975) to a Monod (Michaelis-Menten) equation, modified to include a lower threshold for feeding (Fig. 1). All asymptotic statistics are approximate; hence, variations in the algorithm, the number of iterations, and the starting values can produce different estimates of the nonlinear parameters (Ralston and Jennrich, 1978). Also, the confidence intervals of parameter estimates based on the nonlinear algorithm are obtained by first linearizing the variables and hence are somewhat incorrect. Several solutions of the nonlinear equations for the *Xenopus* data set gave a zero estimate for  $TC$ : for example,  $I_{\max} = 3.6 \pm 1.0 \times 10^9 \mu\text{m}^3 \cdot (\text{g wet mass})^{-1} \cdot \text{h}^{-1}$ ,  $K_{1/2} = 5.2 (\pm 4.6) \times 10^7 \mu\text{m}^3$ , and  $TC = 0.0 (\pm 4.5) \times 10^6 \mu\text{m}^3$ . This result apparently was a statistical artifact: variability in individual feeding "thresholds" resulted in low statistical repeatability. Zero filtering rates were, in fact, measured for several individual tadpoles at positive, measurable yeast concentrations (Fig. 1). None of the nonlinear solutions for the *Rana* larvae gave zero estimates for  $TC$ . The fitted line (Fig. 1) shows the solution giving the smallest estimated threshold for *R. pipiens* tadpoles. Additional solutions with "well-behaved" residual plots included  $I_{\max} = 2.9 (\pm 1.3) \times 10^9 \mu\text{m}^3 \cdot (\text{g wet mass})^{-1} \cdot \text{h}^{-1}$ ,  $K_{1/2} = 2.7 (\pm 3.7) \times 10^8 \mu\text{m}^3$ , and  $TC = 3.3 (\pm 5.4) \times 10^6 \mu\text{m}^3$ , for *R. pipiens*.



TABLE I  
*Estimated parameters for relationships between feeding responses and concentration in anuran larvae (Rana and Xenopus).*

	Below "critical" concentration	Above "critical" concentration
<b>Filtering Rate</b>		
<i>Rana pipiens</i>	$\log FR = -14.63 (\pm 11.55) + 2.23 (\pm 1.76)^* \log C$	$\log FR = 5.17 (\pm 1.82) - 0.50 (\pm 0.24)^{***} \log C$
<i>Xenopus laevis</i>	$\log FR = -18.78 (\pm 24.93) + 3.52 (\pm 4.72) \log C$	$\log FR = 4.20 (\pm 0.93) - 0.37 (\pm 0.13)^{***} \log C$
<b>Pumping Rate</b>		
<i>Rana pipiens</i>	$\log PR = 2.73 (\pm 2.58) + 0.16 (\pm 0.39) \log C$	$\log PR = 4.62 (\pm 1.53) - 0.10 (\pm 0.20) \log C$
<i>Xenopus laevis</i>	$\log PR = 3.91 (\pm 3.11) - 0.07 (\pm 0.59) \log C$	$\log PR = 5.09 (\pm 1.12) - 0.27 (\pm 0.16)^{**} \log C$
<b>Buccal Volume</b>		
<i>Rana pipiens</i>	$\log BV = -16.22 (\pm 10.84) + 2.35 (\pm 1.65)^{**} \log C$	$\log BV = 4.40 (\pm 1.54) - 0.52 (\pm 0.20)^{***} \log C$
<i>Xenopus laevis</i>	$\log BV = -19.08 (\pm 24.01) + 3.46 (\pm 8.44) \log C$	$\log BV = 1.57 (\pm 0.96) - 0.05 (\pm 0.14) \log C$

$H_0: \beta = 0$

\*  $0.05 > P > 0.01$

\*\*  $0.01 > P > 0.001$

\*\*\*  $0.001 > P \geq 0.0001$

Estimates of parameters ( $\pm 95\%$  confidence intervals), from linear regressions on log-transformed data, of several variables related to feeding regulation in obligate (*Xenopus*) vs facultative (*Rana*) suspension-feeding tadpoles. Data in Fig. 1, 2. Parameters estimated from data collected on tadpoles feeding on yeast concentrations above and below the "critical" concentration for each species. Points of inflection on piecewise regressions determined the "critical" concentrations: *R. pipiens*  $7.9 \times 10^6 \mu\text{m}^3 \cdot \text{ml}^{-1}$ ; and *X. laevis*  $6.3 \times 10^5 \mu\text{m}^3 \cdot \text{ml}^{-1}$ .

*Buccal volume as a function of individual size*

The apparent buccal volume ( $BV$ : volume cleared/pump stroke) for *Xenopus* larvae was larger than that for comparably sized *Rana* larvae (Fig. 2). An analysis of covariance, using individual snout-vent length ( $SV$ ) as the covariate, indicated that the *Xenopus* larvae had larger apparent buccal volumes than did the *Rana* larvae, over all size classes examined ( $F = 148.5$ ;  $P = 0.0001$ ). A double-logarithmic transformation of the data indicates that  $\log SV$  vs  $\log BV$  are linearly related (Fig. 3). Therefore, the relationship between  $SV$  and  $BV$  could be fitted to a power function for cohorts of both *X. laevis* and *R. sphenocéphala*. Using nonlinear regression (after Zar, 1968), the parameters in the power function were: *Xenopus*  $BV = 7.63 (\pm 4.03) SV^{1.86 (\pm 0.74)}$ ; *Rana*  $BV = 1.23 (\pm 0.65) SV^{2.38 (\pm 0.86)}$ . The exponents of the two power functions were not significantly different from each other or from 2 ( $P > 0.05$ ). The estimates of the exponents for both species was less than 3, indicating negative allometry (Huxley, 1932, 1950).

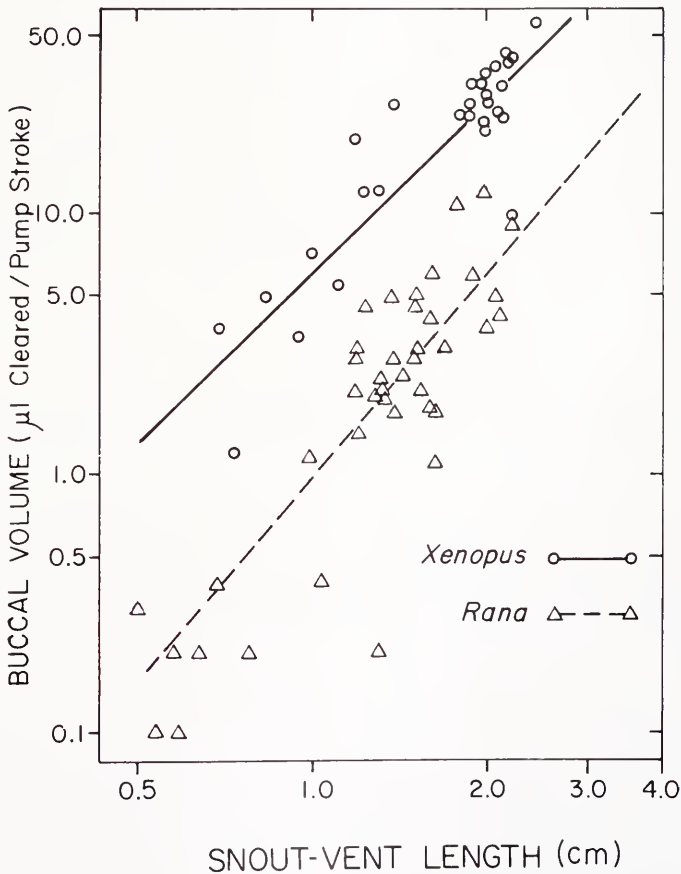


FIGURE 3. Apparent buccal volumes ( $BV$ ) of *X. laevis* and *R. sphenocéphala* larvae, as functions of individual sizes, measured by snout-vent lengths ( $SV$ ). This double-logarithmic transformation of the data indicates that the relationships can be described by power function ( $BV = aSV^b$ ), with  $b < 3$ , suggesting negative allometry.

## DISCUSSION

*Adaptations of obligate and facultative suspension-feeding tadpoles*

Morphological differences between *Xenopus* and *Rana* larvae reflect their obligate and facultative suspension-feeding habits. The *Xenopus laevis* larva is an obligate, midwater suspension feeder, and lacks the keratinized beak, dual water pump, and pharyngeal bypass of the facultative suspension-feeding *Rana* larva (Gradwell, 1971, 1972a, b, 1975; Wassersug and Hoff, 1979; Wassersug, 1980). A keratinized beak enables the *Rana* larva to produce suspensions from attached particles, which then can be ingested. In addition, the *Rana* larva's potential feeding versatility is demonstrated by buccopharyngeal structures which allow great flexibility in adjusting buccal volume (Wassersug, 1980). By altering contractions of the musculature associated with the buccal pump, *Rana* tadpoles can regulate buccal volume over as much as 3 orders of magnitude to adjust to changing particle concentrations (Fig. 2; Seale and Wassersug, 1979; Wassersug and Hoff, 1979).

The *Xenopus* larva has an unusually large buccal volume, large branchial baskets with dense gill filters, and extensive branchial food traps (Wassersug and Hoff, 1979; Wassersug and Rosenberg, 1979; Wassersug, 1980; Seale *et al.*, 1982). Compared to *Rana*, a *Xenopus* larva has a relatively short lever arm on the cartilagenous ceratohyal which delivers the driving force of the tadpole's buccal pump (Wassersug and Hoff, 1979). Hence, a relatively shallow contraction of the buccal pump musculature can cause a disproportionately large volume of water to be displaced in *Xenopus* (Wassersug and Hoff, 1979). This means the *Xenopus* larva can clear a larger volume of water than *Rana*, with each pump stroke. However, the arrangement of cartilage and musculature in the *Xenopus* (contra the *Rana*) tadpole limits its ability to adjust the amplitude of the pump stroke (Gradwell, 1971, 1972a, b; Wassersug and Hoff, 1979; Wassersug, 1980).

*Buccal volumes in growing Rana and Xenopus larvae*

Prior to the onset of metamorphosis, tadpole body proportions remain relatively constant, indicating isometric growth (Wassersug, 1975). However, a closer examination suggests some subtle trends away from isometry in certain body shape parameters. For example, from a geometric model of the tadpole's buccal pump, Wassersug and Hoff (1979) found that buccal volume scales as a power function of snout-vent length, with the exponent less than three, *i.e.* negative allometry. They, however, reached this result from an examination of the morphology of preserved specimens. My results (Fig. 3) with living *R. sphenoccephala* and *X. laevis* larvae confirm this relationship.

*Suspension-feeding dynamics of Rana vs Xenopus larvae*

The qualitative shapes of curves describing relationships between filtering and ingestion rates vs particle concentration, for *Xenopus* and *Rana* larvae, were similar in three major respects (Fig. 1): 1) with increasing particle densities, ingestion rate asymptotically approached a maximum; 2) the filtering rate peaked at an intermediate "critical" concentration; and 3) estimated filtering and ingestion rates declined rapidly from maximum at the "critical" concentration to zero at a lower "threshold" concentration. These feeding curves confirmed previous results, which applied somewhat different methods (Seale and Wassersug, 1979; Seale and Beckvar, 1980; Seale *et al.*, 1982). Hence, these patterns of feeding regulation (Fig. 1)

apparently are characteristics of the animals, rather than experimental artifacts. Furthermore, these patterns were consistent with mathematical equations previously developed to describe zooplankton feeding (further discussion below).

Unlike earlier studies with algae (Seale and Beckvar, 1980), the larvae of *Rana* and *Xenopus* had approximately the same maximum ingestion rates, when fed yeast, adjusted for tadpole mass (Fig. 1). As previously observed (see Seale and Wassersug, 1979), the concentration "threshold" for the *Xenopus* larva was lower than for *Rana*. However, the "threshold" observed for *Xenopus* in this study was lower than that previously obtained (Seale *et al.*, 1982), and was not significantly different from zero (Fig. 1, and associated text). The reasons for these quantitative differences are not clear, but may be related to differences in food quality and methodology.

The precise mechanisms used to adjust filtering and ingestion rates differed in the two species. The larva of *X. laevis* altered filtering rates almost exclusively by varying pumping rate, and the *R. pipiens* larva by adjusting buccal volume (Fig. 2). These observations were consistent with morphological adaptations for feeding (described above), and with preliminary studies (see Seale and Wassersug, 1979; Wassersug and Hoff, 1979; Seale *et al.*, 1982). The *Xenopus* larvae maintained near-maximum filtering rates over a much wider concentration range than *Rana* (Fig. 1), primarily by clearing a larger volume of water with each pump stroke (Fig. 2). Over all size classes, *Xenopus* larvae had larger buccal volumes than comparably-sized *Rana* (Fig. 3).

The obligate suspension-feeding larva of *Xenopus* can survive solely on suspended particles over a wider range of concentrations, but the facultative suspension-feeding *Rana* larva has greater behavioral plasticity in its feeding. *Xenopus* larvae can remove particles at very low concentrations, within the range of those in most oligotrophic lakes (Kalff and Knoechel, 1978). *Xenopus* tadpoles have been observed in eutrophic African ponds (R. Inger, pers. comm.), but energetically they are capable of surviving in more oligotrophic waters (Seale *et al.*, 1982). *Rana* larvae can switch their feeding to fit available food (Seale, 1980). *Rana* tadpoles ingest epiphytic (Dickman, 1968), epibenthic (Calef, 1973), as well as suspended (Seale and Wassersug, 1979; Seale and Beckvar, 1980) microscopic organisms and detritus.

#### *Tadpole feeding compared to predictions of general suspension-feeding models*

Models are valuable only if they can be used as tools for increasing our understanding of important ecological questions, for example: How effectively does the model describe the observed shapes of feeding curves? Are the mechanisms used by the animal to regulate its feeding consistent with the model's assumptions?

Two classes of models describe the general shapes of the feeding curves exhibited by the tadpoles (Fig. 1 and description above): 1) "curvilinear" models, modified to include a lower concentration "threshold" below which feeding ceases; examples are models which assume a rectangular hyperbola (Michaelis-Menten or Monod) or a negative exponential (Ivlev) equation, both of which predict that feeding will approach a maximum asymptotically at high concentrations (see Mullin *et al.*, 1975); and 2) models which assume suspension feeders adjust ingestion to maximize energy return at each food concentration (Lam and Frost, 1976; Lehman, 1976). Tadpoles regulate their feeding by complex, species-specific, behavioral adjustments (Fig. 2), which probably can be understood best in terms of energy requirements. The shapes of the feeding curves relating  $I$  and  $F$  to  $C$  compare extremely well

with predictions for the simple modified Monod model (Fig. 1), and fairly well with the more complex energy optimization models. The major difference is that the energy optimization models do not predict an absolute feeding "threshold," such as that observed in tadpoles (Fig. 1). Instead they predict a reduction in filtering and ingestion to low, positive rates, as concentrations decline (Lehman, 1976). Doyle (1979) has demonstrated that energy optimization models are mathematically compatible with the simple Monod model. Both may be derived from an assumption of regulation by gut satiation: this could be a fundamental regulatory mechanism for suspension feeding, leading to similar feeding patterns in phylogenetically diverse animals.

Tadpoles can make behavioral adjustments to compensate for reductions in particulate food: 1) pumping rates (hence energy expenditures) decline in animals after at least 1 h of being acclimated to very low particle levels (Seale *et al.*, 1982); and 2) animals may move to higher particle concentrations. Seale *et al.* (1982) suggested that as particle levels decline to a  $C$  near the observed "threshold," the energy expended by a tadpole in filtering suspensions probably would not be balanced by energy gains, providing an impetus for a behavioral shift in feeding regime (also see below).

The modified Monod model can be derived from several biologically reasonable assumptions concerning mechanisms for feeding regulation: 1) Feeding surfaces can become "saturated." The asymptote in the feeding curve (maximum ingestion rate) corresponds to highest concentrations, where filtering surfaces become filled (Parker, 1975; Real, 1977). 2) Ingestion rate is governed by prey densities and predator search time (related to encounter probability) and handling time (after Holling, 1959, 1965; Crowley, 1973). 3) Feeding can be governed by gut-filling rate or satiation (Doyle, 1979). Although none of these mechanisms have been shown conclusively to operate for tadpoles, they are consistent with what is known about tadpole feeding (see Seale and Wassersug, 1979; Seale *et al.*, 1982). For example, tadpole filters show no signs of particle accumulations except at very high concentrations (Seale *et al.*, 1982), consistent with assumption 1.

The rectangular hyperbola is mathematically isomorphic with Holling's (1959, 1965) "invertebrate predator" or "Type II" functional response (Parker, 1975; Real, 1977). The "Type III" or "vertebrate predator" model, a sigmoidal feeding function, is similar in shape to feeding curves predicted by energy-optimization models (Lehman, 1976), and represents the effects of learning and of alternative prey on animal feeding, shifting from the "Type II" curve (Real, 1977). Tadpole feeding cannot be described accurately with the "rectilinear" model of Rigler (1961), the algebraic analog of Holling's "Type I" or "suspension feeder" model, because: 1) tadpole filtering surfaces are not saturated at the "critical" concentration (Seale *et al.*, 1982); and 2) tadpole filtering rates decline below the "critical" concentration, rather than remaining constant as Rigler assumed. Obviously, Holling's (1959, 1965) phylogenetic and functional categories for these models are restrictive, although the models themselves are useful for describing general feeding responses.

The "threshold" in the modified Monod model could represent either a discontinuity in feeding (as in Fig. 1), or a behavioral response to environmental heterogeneity. The data indicate that individual tadpoles can reduce feeding rates to zero at low concentrations (Fig. 1), but these indirect feeding data cannot determine if this "threshold" represents an actual reduction in filtering rate, a "compensation point" where ingestion is balanced by particle release, or a reduction in entrapment efficiency (Seale, 1981). Theoretically, "threshold" feeding behavior also can rep-

resent the case where a predator becomes inactive or less efficient at low concentrations. In addition, the threshold in the modified Monod model provides a simple first approximation to a mathematical expression of the potential effects of a facultative suspension feeder on planktonic organisms, e.g. the ability of the *Rana* tadpole to switch feeding from the water column to the sediments or other alternative food sources at low particle concentrations (Seale, 1980). This equation could also be used as a simple model of other discontinuities in feeding, such as migration to a more concentrated patch in a heterogeneous environment, or a temporary inability to ingest prey in a spatial refuge which can become available for predation (e.g. algae attached to substrates may later become suspended).

Although the modified Monod model describes tadpole feeding data fairly well (Fig. 1), "parameters" in the model are somewhat sensitive to individual variability, past history, and environmental conditioning (also see Donaghay and Small, 1979). In these studies, non-zero "thresholds" were observed on individual larvae (Fig. 1). However, the "threshold"  $C$  varied from tadpole to tadpole. This individual variability probably was a factor causing the population parameter estimate for the threshold to be zero for some nonlinear regressions. Measurements made on many animals at once (as in zooplankton feeding studies: Mullin *et al.*, 1975) should not be expected to provide unambiguous parameter estimates for a "threshold," even if one exists.

Individual variability aside, "parameter" estimates for feeding models cannot be interpreted as physiological constants for the species. For example, the pumping rates of tadpoles acclimated 1 h to one  $C$  were lower than for other tadpoles experiencing that same  $C$  while causing continuous reductions in particle concentrations (Seale *et al.*, 1982). In continuous reduction experiments, tadpoles maintain maximum pumping rates at very low  $C$  (Seale *et al.*, 1982; Fig. 2, this study), which probably causes the apparent  $K_{1/2}$  to be somewhat lower than would be seen in well-acclimated tadpoles. F. M. Williams (unpubl.) has predicted such a distortion in the feeding curve when feeding effort remains disproportionately high at relatively low concentrations, and has named this the "Avis Effect" ("We try harder"). Using a flow-through system, Seale (unpubl.) also has shown that tadpoles exhibit higher pumping rates at given  $C$  after having been maintained for some time in low  $C$ , compared to rates observed after tadpoles were held in higher  $C$ . Feder (1981) demonstrated that for *Xenopus* larvae a number of factors, including time of day and stress from physical disturbances, can cause dramatic changes in respiratory activities, which are linked to feeding in tadpoles. Nevertheless, when measured under similar experimental conditions, differences in feeding parameters may be useful in comparing relative feeding capabilities, as for evaluating potential competitive interactions among different species and sizes of tadpoles (see also Seale, 1980, 1981; Seale and Beckvar, 1980).

#### *Evolutionary considerations and the impact of vertebrate suspension feeders on plankton*

A *Xenopus* larva can clear a much larger volume of water with each pulsatile contraction of its buccopharyngeal musculature than can a *Rana* larva. Hence, the *Rana* larva must pump more rapidly to obtain the same amount of food at any given concentration (Figs. 1, 2). Because of its slower pumping rate (Fig. 1), the energy expended by the *Xenopus* larva probably is less than that needed by the *Rana* larva to obtain a comparable amount of food at any given particle concentration.

These deductions suggest a partial explanation for the differences in feeding regulation in *Xenopus* compared to *Rana* larvae, assuming such differences reflect adaptations to the environment. Because of low seasonal variability, primary production tends to remain relatively high and constant through time in South African, compared to temperate, waters (Greenwood, 1976). The *Xenopus* larva is endemic to South Africa. Over evolutionary time, an environment with a dependable source of suspended particles should justify the extra energetic costs needed to maintain this larva's elaborate feeding structures (see also Wassersug, 1980; Seale *et al.*, 1982). No anurans with obligate suspension-feeding larvae are endemic to temperate North America. The same morphological specializations which enable a *Xenopus* larva to maximize the volume cleared per pump stroke lead to inflexibility in the intensity of the pump stroke (Wassersug and Hoff, 1979; Wassersug, 1980). Extreme variability and unpredictability of particulate densities characterize the temperate environments inhabited by facultative suspension-feeding anuran larvae, such as *Rana* tadpoles. The ability to adjust pump stroke intensity allows them to adjust the energy costs associated with suspension feeding. In addition, their greater flexibility in feeding behavior improves their ability to adapt to a more unpredictable environment (additional discussions above and in Wassersug, 1975, 1980; Seale, 1980). Tadpoles overwintering in temperate habitats encounter low primary production rates but can exploit alternative foods (Seale, 1980). The *Rana* larva's ability to shift grazing may be related, at least in part, to predator avoidance. In the presence of predation, the *Rana* larva can feed on alternative foods, whereas the *Xenopus* larva is constrained to remain in the water column. This may imply a fundamental difference in adaptations to avoid predation in these two species. In support of this hypothesis, the *Xenopus* larva is transparent whereas North temperate tadpoles, such as *Rana*, tend to be colored cryptically, *e.g.* to blend in with the sediments.

One may speculate on the probable trophic dynamics in ecosystems dominated by large vertebrate suspension feeders. All such animals, including tadpoles, are several orders of magnitude larger than their planktonic prey. For example, an average *Xenopus* larva weighs  $10^4$ – $10^5$  times as much as an average copepod, but can ingest prey of the same size taken by copepods, or smaller. Since these vertebrates feed on lower trophic levels than most, the number of links in the food chain is reduced, potentially leading to high trophic efficiencies. Circumstantial evidence for unusually efficient transfer of energy from autotrophs to vertebrates have been noted in ecosystems dominated by tadpoles (Seale, 1980) and by planktivorous fishes (Hecky and Fee, 1981; Hecky and Kling, 1981). In both ecosystems, algal standing crops were about an order of magnitude lower than expected to support these vertebrate populations, if trophic efficiencies were "normal." At times vertebrate biomass exceeded phytoplankton biomass (Seale, 1980; Hecky and Fee, 1981). Assuming gut contents comprise 30–50% of a tadpole's biomass (after Calef, 1973; Feder, 1981), during these trophic "inversions" the algal biomass inside tadpoles at times equalled or exceeded that in the water column (Seale, 1980). At maximum tadpole densities, the estimated rates of material flux through the *Rana* larvae exceeded the total (per pond) rates of primary production (Seale, 1980). These field observations cannot distinguish between high trophic efficiencies and additional sources of energy for the vertebrates, such as chemoautotrophic and heterotrophic production by bacteria (Hecky and Kling, 1981). The tadpoles released large amounts of dissolved organic matter, which could have promoted bacterial growth and/or inhibited algal growth (Seale, 1980).

A number of adult or larval aquatic vertebrates can entrap plankton several orders of magnitude smaller than their own body mass. Examples are larval lampreys (Moore and Mallatt, 1980), filter-feeding fishes (Durbin and Durbin, 1975), baleen whales (Brodie, 1975), and tadpoles. Some patterns of behavior exhibited by these animals represent adaptations to variability in rates of supply of particulate food, among other factors. Seasonal variability in levels of such particles may have been an important evolutionary impetus for the development of metamorphosis in anurans (Wassersug, 1975). An intriguing analogy may be drawn between metamorphosis in vertebrates with suspension-feeding larvae, such as anurans and lampreys, and migratory behavior in other suspension-feeding vertebrates, such as whales and fish. Some cetaceans, such as the fin whale, filter huge quantities of seasonally available krill from Antarctic waters during a few months each year; blubber stored during these summer excursions then supplies energy for migrations into warmer waters, where food is limited but maintenance energy requirements are minimal (Brodie, 1975). Adult mullets are open-water oceanic fish which lay their eggs at sea. The hatchlings then migrate into estuaries where they feed on suspended plankton in this highly productive habitat for about a year (Bardach *et al.*, 1972). Lamprey have suspension-feeding larvae which take advantage of seasonally abundant suspended particles in freshwater streams, but as adults are parasitic on fish (Moore and Mallatt, 1980).

The first vertebrates almost certainly were suspension feeders (Romer, 1970). Divergence from this feeding mode probably was stimulated, in part, by the vertebrates' comparatively slow population responses to variations in particulate food. In contrast, zooplankton populations may respond within hours to variations in particulate food, for example, by changing egg production, hatching success, developmental time, adult size, reproductive mode (sexual vs asexual), and life span (Boraas, 1980). A number of behavioral adjustments, such as migration, metamorphosis, threshold feeding, and prey switching, may serve to minimize overexploitation of the prey of vertebrate suspension feeders, while insuring adequate food to supply energetic needs.

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